The Identity of *Cribrilaria innominata* (Couch, 1844) (Bryozoa, Cheilostomata)

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Synopsis

The universally accepted identity of *Lepralia innominata* Couch, 1844, i.e. that of a cribrilinid species commonly placed in the genus *Cribrilaria,* was established by Johnston in the second edition (1847) of *A History of the British Zoophytes* but may not have been that intended by Couch. In the absence of the type series, from which the true nature of the species might have been determined, Johnston's concept of the taxon is accepted and a neotype is selected from his material. A redescription based on the neotype is given. It is hoped thereby to restrict and stabilise the usage of the name, which has been applied to a number of Recent and fossil cribrilinid species. The occurrence of the species as a fossil in the European Neogene is regarded as unproven; a record from the Pliocene Crags of eastern England is specifically rejected.

Introduction

Studies in the last few years have revealed considerable present-day diversity within the cribrimorph genus *Cribrilaria,* particularly in the NE. Atlantic region (Harmelin, 1970; 1978; 1984). This realisation has accompanied a narrowing of species concepts within the genus, necessitating a re-examination of the commonly-cited older nominal species in order to establish their precise identity. Following the view of Hincks (1880), *Cribrilaria innominata* (Couch, 1844) was regarded by many workers as merely a form or variety of *C. radiata* (Moll, 1803). Recently, however, the separate identity of the two species has been reaffirmed, for instance by Harmelin (1970) and Hayward & Ryland (1979). The apparent intergradation exhibited by *C. radiata* and *C. innominata* seems to have resulted, at least in part, from the confusion of several species under each name. A neotype of *C. radiata* was selected by Harmelin (1970) who also distinguished two forms, A and B, of *C. innominata.* Harmelin attributed a relatively restricted geographical distribution (perhaps exclusively Mediterranean) to *C. radiata,* but regarded *C. innominata* as cosmopolitan. Gordon (1984) also considered *C. innominata* to be cosmopolitan. However, type material of *C. innominata* has not been recognised, and it seems highly probable that the name is still being used for several different but related species. The present paper is an attempt to examine the origin of the concept of *Cribrilaria innominata* and to clarify its identity by reference to type material.

Development of the concept of *C. innominata*

The original description and figure (R. Q. Couch, 1844) of *Lepralia innominata* are inadequate to define the species. There is, indeed, little to suggest a cribrimorph identity for the taxon. Couch did not place any other taxon in synonymy with his new species. The provenance of his material was given as 'On stones, rare. Goran, *Mr. Peach.* Polperro. Mount's bay' (Couch, 1844: 114). Charles W. Peach's assistance in providing specimens for Part 3 of *A Cornish Fauna* was warmly acknowledged by Richard Couch (1844; iv–v, preface dated August 1844). Peach worked as a Customs Officer in Cornwall; from October 1834 to March 1845 he was based at Goran (or Gorran) Haven, south of Mevagissey, then he moved to Fowey before transfer to Scotland in December 1849 (Boase & Courtney, 1878; Lee, 1895).

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Peach himself announced the discovery of two new species of *Lepralia* to a meeting of the British Association for the Advancement of Science, at York in September 1844. The published summary of his communication (Anon., 1845: 65) cited these as '*Lepralia catenata* and *Lepralia pectinata,* which [Peach had stated] Dr. Johnston of Berwick-on-Tweed and Mr. Couch of Penzance have pronounced new and good species'. No descriptions or figures were given and, if this report (in the third person, by an anonymous editor) of his remarks qualifies as a publication of the names by Peach, they must be regarded as *nomina nuda.* The report of the Royal Institution of Cornwall for 1845 lists donations to their Museum for the period 3 December 1844 to 7 November 1845. These included specimens of 18 species of coelenterates and bryozoans from Goran and Fowey Harbour presented by Peach; amongst them were *Lepralia catenata* and *L. pectinata,* but not *L. innominata. (L. catenata* was *Chorizopora brongniartii* (Audouin) according to later authors. *L. pectinata* will be discussed below.) Peach's donation did not include material referred to any of the new species described by Couch (1844). None of Peach's bryozoan specimens are now to be found in the collections of the Royal Institution of Cornwall (R. D. Penhallurick, Assistant Curator, pers. comm., 1985).

Johnston (1847) redescribed *Lepralia innominata* in his *History of the British Zoophytes.* In the preface to this work (i.e. to the second edition) he acknowledged the assistance of both Peach and Couch. However, Peach's name alone was placed after the diagnosis of *L. innominata,* the significance of this convention being explained by Johnston (1847: 30, footnote) as follows: 'The name affixed to the specific character is that of the person who, so far as I have been able to ascertain the fact, added the species to the British Fauna'. Johnston placed 'Lep. pectinata, *Peach* MS' in synonymy with *L. innominata*; his listed material of the species was provided by Peach from Cornwall and by G. C. Hyndman from W. Scotland. Johnston's diagnosis, description and figure (1847: 319–320 and pl. 55 fig. 12) appear to contradict those of Couch (1844: 114–115 and pl. 22 fig. 4) on several points. Thus 'cells short, sub-orbicular or ovate' (Johnston) contrasts with Couch's figure showing slender zooids about three times as long as broad (although Couch's own text also says 'oval'). Johnston states 'aperture ... armed with several short denticles or spines not longer than its diameter' (perhaps describing spine bases left after spines had been lost) whereas Couch indicates long oral spines clearly exceeding the dimensions of the orifice. Most significantly, Johnston specifies ridges on the zooids radiating from the midline, but Couch describes and illustrates a series of short, sub-parallel transverse bands. Perhaps not surprisingly, Johnston characterised Couch's figure (and description?) as 'very bad'. The cribrilinid concept of *L. innominata* adopted by later workers seems clearly to have been established by Johnston rather than Couch. However, Johnston's account is insufficient to allow the separation of one particular species from other, related, cribrimorphs.

A large collection, presented by Johnston to the British Museum in 1847, was described in the handwritten accessions book as 'The authentic specimens from which the descriptions in "Johnston's British Zoophytes" were taken'. Material of *L. innominata* from the locations listed by Johnston (1847) is represented by only two specimens: BM(NH) 1847.9.16.32 (Goran, Cornwall, C. W. Peach—a label with the specimen indicates that this was collected in September 1843) and 1847.9.16.122 (Sana Island, W. Scotland, G. C. Hyndman). These specimens are conspecific; they are both labelled *L. pectinata* in Johnston's handwriting. The collection included six additional specimens listed in the accessions book as *L. pectinata* (as were the two just mentioned), for which the locality was given simply as 'British'. This poorly localised material was not specifically referred to by Johnston (1847). Some of these specimens are conspecific with those from Cornwall and Scotland; others belong to a closely related (possibly conspecific) form of similar zooidal dimensions sharing the large suboral lacuna regarded as characteristic of *L. innominata* by later authors, but differing in details of the frontal wall calcification. The status of the latter form will not be further discussed here.

Busk (1854: pl. 86 fig. 2) illustrated *Lepralia innominata* from one of Johnston's specimens, 1847.9.16.32, collected at Goran Haven by Peach. This was the most detailed and informative figure of *L. innominata* yet published, clearly showing a distinct triangular area, proximal to the D-shaped orifice, pierced by a large suboral pore or lacuna. Busk's diagnosis of the species also noted this suboral pore. *Lepralia pectinata* Peach MS was listed in the synonymy for the species.

In addition, Busk provided a second figure of *L. innominata* (pl. 86 fig. 3). The illustrated specimen, 1847.9.16.79, was also part of Johnston's collection. However, there is no record that Johnston himself identified this colony as *L. innominata*. The colony encrusts a bivalve shell also colonised by several other species of bryozoan; Johnston's labels, and the accession details, refer to these other species only. The species illustrated in pl. 86 fig. 3 would today be placed in the genus *Puellina*; it agrees with the description by Hincks (1880: 186) of *Cribrilina radiata* var. *a*, which has been taken to be *Puellina setosa* (Waters).

Busk (1860: 282) later noted the possibility that *L. innominata* (referred to as '*L. innominata*, Johnst.') might be a synonym of *Eschara radiata* Moll, 1803, a species described from the Mediterranean Sea. Smitt (1873: 22–23) transferred both species to the genus *Cribrilina* but discounted the possibility of synonymy, giving 'the presence, on *Cribrilina innominata*, of a lunate pore in the triangular or semicircular space, proximally of the zooecial aperture' as a character distinguishing the two species.

Hincks (1880: 185) dismissed Couch's figure (and description?) as 'worthless' and followed Johnston (1847) and later authors in his concept of *Lepralia innominata*. Hincks regarded the species, referred to (1880: 187) as *'Lepralia innominata*, Johnston', as merely a form of *Cribrilina radiata* (Moll). His confusing account recorded both the '*radiata* form' and the '*innominata* form' from Britain. The two forms were considered to intergrade.

Peach (1882) updated the work of Couch (1844) by adding subsequent Cornish records and revising nomenclature with reference to Hincks (1880). *Lepralia innominata* Couch, 1844 was listed in synonymy with *Cribrillina radiata* (*lapsus pro Cribrilina*), thereby endorsing Hincks' treatment of the species. *L. pectinata* was not mentioned.

The genus *Cribrilaria* was founded by Canu & Bassler (1928; 1929: see Lagaaij, 1952) with *C. radiata* as type-species; it was regarded by Gordon (1984) as a sub-genus of *Puellina* Jullien, 1886.

From all this it is apparent that the accepted concept of *Cribrilaria innominata* may not be that intended by Couch (1844), but was established later by Johnston (1847) and partially clarified by Busk (1854) and Smitt (1873). Johnston apparently based his concept of the taxon on Peach's undescribed *Lepralia pectinata,* but treated this as a synonym of Couch's *L. innominata*. The source of Johnston's belief that *L. innominata* and *L. pectinata* were conspecific has not been ascertained. Peach reportedly checked the identity of *L. pectinata* as a new species with Couch during or before 1844 (Anon., 1845), but also provided part of the type material for *L. innominata*. The name *L. pectinata* was not mentioned by Couch (1844), but was apparently still being used by Peach and Johnston in a public talk and for the labelling of specimens around the time of publication of Couch's paper. Peach (1882) accepted Hincks' (1880) treatment of *L. innominata*, implying that he did not question the concept of the taxon that then prevailed.

Non-availability of original type material

A Cornish Fauna, of which Richard Couch's account of the 'zoophytes' formed Part 3, was subtitled 'Intended to form a Companion to the Collection in the Museum of the Royal Institution of Cornwall'; it was published in Truro by the Institution. Type material of *L. innominata* might therefore be sought in the Institution's Museum. In the faunal lists of Parts 1 and 2 (J. Couch, 1838; 1841), species represented in the Museum collection were marked with an asterisk. However, no such convention was adopted for Part 3. This may imply that little relevant material was present in the collection at the time. The present author has been unable to find any record in the Institution's Reports from 1829 to 1871 of the accession to their Museum of a substantial collection of 'zoophytes' that might have been the basis for Richard Couch's work. The Reports for this period include detailed lists of donations compiled approximately once a year; major purchases are noted in the body of the Report. Clear mention is made of material relating to Parts 1 and 2 (particularly in Reports for the years 1837, 1838, 1840 and 1850).

The collection of the Institution's Museum was moved to new buildings during 1917 and 1918. Some time before this move was scheduled to be completed, the former premises were commandeered by the Army Council and it was necessary to vacate the old building hurriedly (as detailed

in the Report for 1918). Time did not permit the orderly relocation of the remaining collections, and a mass of material was stored in the basement of the new premises. Much of this material had not yet been unpacked when a flood destroyed it during the 1950s. None of Richard Couch's 'zoophyte' specimens are now to be found in the collection of the Institution (R. D. Penhallurick, Assistant Curator, pers. comm. to P. J. Chimonides, 1976 and to P. F. S. Cornelius, 1977). Any part of Couch's collection at the Royal Institution of Cornwall (if such a collection existed) that survived into the 1950s was apparently destroyed by the flood.

A second possible location for material studied by Couch would have been the small Museum of the Penzance Natural History and Antiquarian Society. Richard Couch lived in Penzance, and held the honorary post of Curator of the Museum from 1845 to 1855 (as shown by the Society's Reports). However, the Museum no longer exists, and its collections have been scattered and, in part, destroyed. No bryozoan collection attributable to R. Q. Couch is now to be found amongst material known to have been transferred from the Society's Museum, either to Penlee House Museum (Penzance) or elsewhere (Stella M. Turk, Biological Records Unit, Institute of Cornish Studies, pers. comm., 1985).

Couch did not mention *Lepralia innominata* in his subsequent papers. It is concluded that no recognisable type material of *L. innominata* survives.

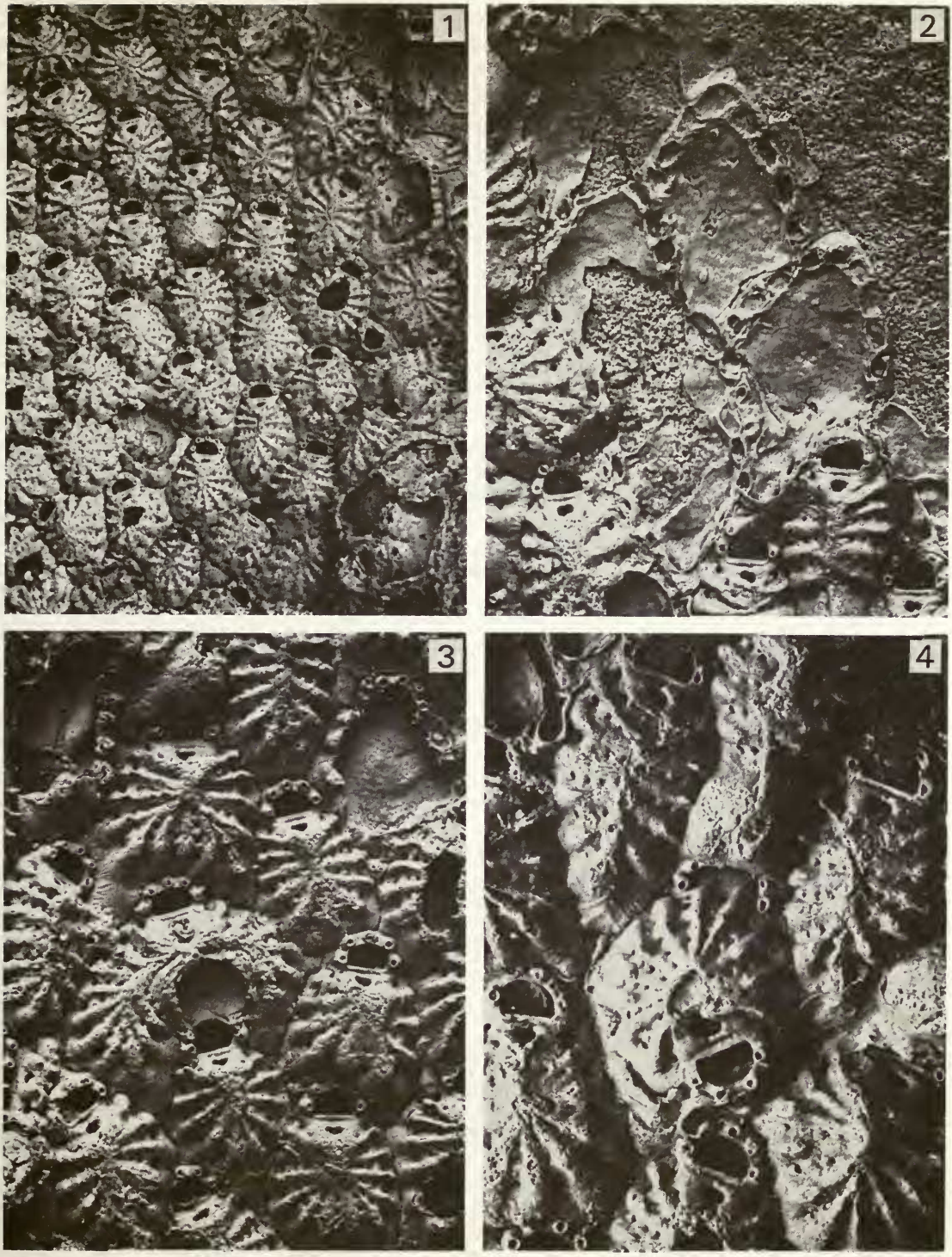
Selection of neotype

In the absence of material from the type series, there seems to be no hope that the true identity of Couch's taxon can ever be determined. The present paper therefore establishes a neotype for *Cribrilaria innominata* in accordance with accepted usage of the name. Since the specimen selected came from one of the type localities of Couch's species, was amongst those before Johnston (1847), and was one of those illustrated as *L. innominata* by Busk (1854), it is hoped thereby to ensure the stability of the name. The author is not aware that this choice of neotype results in any other nominal taxon passing into synonymy with *C. innominata*. A redescription of the species based on the neotype is provided in an attempt to define the species precisely and thus facilitate future revisory work.

The colony encrusting a shell registered as BM(NH) 1847.9.16.32 is selected here as the neotype of *Lepralia innominata* Couch, 1844; the specimen was part of the Johnston collection donated to the British Museum in 1847. Only two of the labels accompanying the specimen appear to pre-date its donation. They read: 'Goran. Sep. 1843 Lepralia pectinata' (with small sketch of two zooids) and '64d Lepralia pectinata' (with the BMNH registration number added in different handwriting). The first label was very probably written by C. W. Peach. The second is in Johnston's handwriting. The specimen is believed to be part of the material listed as *Lepralia innominata* by Johnston (1847); it was listed by Gray (1848: 121) as specimen 'a' of *L. innominata*; it was illustrated, again as *L. innominata*, by Busk (1854: pl. 86 fig. 2; *cf.* present paper, Fig. 1). The single colony, *c.* 5 × 5 mm, encrusts the inner (concave) surface of a broken *Venerupis pullastra* (bivalve mollusc) shell, close to its dorsal margin. It is situated between the tube of a serpulid polychaete (*Pomatoceros* sp.) and the colony of another cheilostome bryozoan, *Escharoides* sp., which was also illustrated by Busk (1854: pl. 88 fig. 5), as *Lepralia coccinea*. Many of the zooecial chambers of the cribrimorph are occupied by a folliculinid ciliate (Figs 7, 8), indicating that most or all of the colony was dead at the time of collection. The colony has *c.* 200 autozooids, of which *c.* 45 are ovicellate. There are five avicularia, three of which are badly damaged.

Redescription of *Cribrilaria innominata* based on the neotype

Colony encrusting, consisting of single layer of clearly delimited zooids. Frontal wall of autozooid convex in transverse section. Shape of autozooid in frontal view variable: often irregular-ovoid, sometimes broadly bifid proximally (with duplication of radiating pattern of costae) when



Figs 1–4 Scanning electron micrographs of *Cribrilaria innominata*, neotype (1847.9.16.32): (1) part of colony × 39, the left-central ovicellate zooid and those surrounding it being those illustrated by Busk (1854); (2) pore chambers visible in damaged zooids × 73; (3) proximally bifid zooid with duplication of radiating pattern of costae × 72; (4) regenerated zooid with oblique polarity axis × 105.

Table 1 Measurements on neotype, in mm, excluding periancestrular zooids

	Range	Mean	No. of Observns	Comments
Length of autozooid	0·35–0·53	0·44	30	Up to 0·63 if long proximal extension of gymnocyst present. (Measurement excluded ovicell if present.)
Width of autozooid	0·24–0·38	0·30	30	Up to 0·58 in proximally bifid zooids
Length of orifice	0·05	—	28	Rarely 0·06
Width of orifice	0·08–0·09	—	29	Rarely 0·10.
Length of ovicell	0·15–0·20	—	10	—
Width of ovicell	0·18–0·21	—	10	—

passing to either side of proximal zooid (Fig. 3). Exposed lateral gymnocyst narrow. Proximal gymnocyst more extensive, often forming narrow proximal extension(s) between neighbouring zooids. Pericyst (= costate frontal shield) with nine to 14 costae (most commonly 12; fewer in periancestrular zooids; up to 16 in proximally bifid zooids). Costae raised, distinct, each with steeply inclined basal portion bearing minute pelmatidium (Fig. 7); variably developed tubercle or short ridge borne at angle of basal portion of costa and more shallowly inclined subsequent portion. Pericyst with blunt suboral median mucro passing into variably developed median ridge. One to three (? rarely four) very small intercostal pores between successive costae; additional single larger pore, with distinct lip along basal margin, between bases of successive costae.

Orifice (Fig. 6) D-shaped, broader than long, proximal edge straight. Five evenly-spaced spine-bases around lateral and distal margin of orifice in non-ovicellate autozooids (only four in one regenerated zooid, Fig. 4). Ovicellate zooids with two closely-spaced spine bases on each side of orifice (the more distal sometimes partially obscured by ovicell). Strongly inclined triangular area between orifice and umbo (not included in counts of costae given above), pierced by large lacuna of variable shape. Each autozooid with three or four pairs of distolateral pore chambers plus one distal pore chamber (? sometimes double) (Fig. 2). Uncalcified external openings of pore chambers (seen in zooids on edge of colony) relatively large, as wide as or wider than calcification separating them.

Ovicell roughly globular, often partially embedded in distal autozooid, with variably developed low ridges or elongate tubercles in more or less radiating pattern on frontal surface, but no pores; median suture line sometimes discernible (Fig. 5). Avicularium (Figs 7, 8) interzooidal, without pivotal bar; rostrum elongate-triangular, edges converging towards tip at angle of *c.* 25–30°, slightly raised (i.e. neither closely adpressed to frontal wall of adjacent autozooid nor lying along interzooecial sulcus). Combined length of palate and frontal non-calcified area *c.* 0·17 mm (two measurements only); proximal gymnocyst of avicularian chamber clearly shorter than this. Ancestrula obscured.

Discussion

Successive generations of bryozoologists have shown a remarkable willingness to indulge in debate on the status and identity of *Lepralia innominata* without pausing to define the species adequately by reference to type material. As a result, many of the numerous records in the

Figs 5–8 Scanning electron micrographs of *Cribrilaria innominata*, neotype (1847.9.16.32): (5) part of colony viewed at angle to emphasise surface sculpture × 72; (6) orifice of autozooid × 350; (7) avicularium and adjacent autozooids × 137, arrows indicate pelmatidia; (8) avicularium (same zooid as Fig. 7) × 230, arrows indicate folliculinid ciliates in orifices of adjacent autozooids (also visible in Fig. 7).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literature of this supposedly cosmopolitan species are at best equivocal, yet may not be firmly discounted without examination of source material. However it can be stated that, amongst records from Recent seas, Busk (1854: pl. 86 fig. 3 only) and Manzoni (1871) do not refer to *Cribrilaria innominata* as defined by the neotype. Similarly, from the respective descriptions, *Colletosia innominata* subsp. *bifida* d'Hondt, 1970 and *Puellina innominata* var. *vicariata* Waters, 1923 do not in fact belong within *Cribrilaria innominata*. The fossil species *Lepralia mitrata* Seguenza, 1879 and *L. elegantissima* Seguenza, 1879 were both referred to *Cribrilina radiata* form *innominata* by Hincks (1884). Comparison of Seguenza's figures (1879: pl. 15 fig. 8 and pl. 8 fig. 11) with the neotype of *Cribrilaria innominata* clearly indicates the rejection of this synonymy (a conclusion already reached by Neviani (1900) in the case of *L. elegantissima*). The record of *Lepralia innominata* from the Pliocene Coralline Crag of eastern England by Busk (1859) is discounted; the accuracy of the published account was checked in this case by examination of part of the relevant material (BMNH B1697, D6754, D6799 and D6934). Since Manzoni (1869) based his concept of *L. innominata* on Busk's (1859) account and apparently copied Busk's figure, his record from the Italian succession must also be questioned. Indeed, the occurrence of *Cribrilaria innominata*, as defined by the neotype, as a fossil in the European Neogene is regarded as unproven.

The account of *Cribrilaria innominata* given by Hayward & Ryland (1979) agrees in all relevant details with the neotype. BM(NH) 1899.5.1.723, from which at least part of Hayward & Ryland's figure was drawn, is considered to be conspecific with BM(NH) 1847.9.16.32.

The neotype colony shows an example (Fig. 4) of 'total regeneration with oblique polarity axis' *sensu* Jebram (1978: 259 and fig. 4). In this case, the regenerated zooid appears to have been budded from the left distolateral neighbour of its damaged predecessor; it is abnormal in having four rather than five oral spine bases.

The proximally bifid zooids found in the colony (Fig. 3) may represent 'lateral cystid fusions' *sensu* Jebram (1978: 260 and fig. 4). It is probable that three parent zooids (one proximal, two proximolateral) contribute to the development of a bifid zooid. In the observed examples, the orifice shows the same orientation as those of surrounding zooids. An example of a bifid zooid with the orifice oblique (i.e. aligned with one of the proximal branches of the zooid) in an Upper Cretaceous cribrimorph is illustrated by Jebram & Voigt (1977). These authors also list other fossil occurrences of 'heart-shaped' zooids recorded in the literature. In less well developed cases, cribrimorph zooids may simply show extreme proximal widening with partial duplication of the radiating pattern of costae. Waters (1923: 558) recorded specimens referred to *Puellina innominata* 'with the proximal part [of some zooids] spreading out' and cited a similar occurrence in *Castanopora castanea* illustrated by Lang (1922: pl. 5 fig. 2). Proximally bifid zooids and zooids with extreme proximal widening appear to be relatively common in cribrimorphs.

As noted in the redescription above, the most peripheral of the pores between adjacent costae differ in size and morphology from the others. They may prove to be bounded on their outer or more basal margin by gymnocyst rather than intercostal calcification. The term intercostal pores should not, perhaps, be used to include these outer pores. Norman (1903: 96–98), noting that they were distinct, used the term 'papillae-pores' (or 'papillae-holes'), since a series of uncalcified papillae emerge through them (in material in which soft parts are preserved); the most distal and longest pair of these are commonly called setiform papillae. The papillae are found in many species of *Cribrilaria* and *Puellina*, and were cited in the diagnosis of *Puellina* by Levinsen (1909) and Gordon (1984). They were discussed by Smitt (1873), Harmer (1902; 1926), Norman (1903), Levinsen (1909), Waters (1923), Canu & Bassler (1928) and Gordon (1984), and illustrated using SEM by Harmelin (1970: pl. 2 fig. 5; 1984: figs 4, 5, 6 and 7).

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